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The Iguanid Lizard Genera *Urosaurus* and *Uta*, with Remarks on Related Groups

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(Text-figures 1-6)

In the course of studies leading toward a re-evaluation of the supraspecific units within the lizard family Iguanidae it seems expedient to pause from time to time and make available portions of the completed work. It is hoped that these progress reports can eventually be correlated with additional material to form a comprehensive revision of the family. This paper is the second of a series pertaining to the systematics of the Iguanidae.

Statement of the Problem

Until recently all North American iguanids with a well-developed gular fold, a large rostral scale, non-imbricate supralabials, imbricate supercilliaries, large and regularly arranged upper head shields, a large interparietal scale, a well-defined ear-opening, sternal fontanels and with the parietal organ consistently piercing the parietal bone posterior to the suture between the frontal and parietal bones, have been placed in the genus *Uta* Baird & Girard, 1852. Mittleman (1942) suggested that this assemblage was artificial and purported to demonstrate that the group was actually comprised of four distinct genera, *Petrosaurus* Boulenger, 1885; *Streptosaurus* Mittleman, 1942; *Urosaurus* Hallowell, 1854; and *Uta* Baird & Girard, 1852. Although the differences used by Mittleman to separate these groups were of questionable significance, support for the division of *Uta* was provided by his ideas of the phylogeny of the North American iguanids. This supposed natural subdivision of the Iguanidae traditionally has included the following genera: *Callisaurus* Blainville, 1835; *Crotaphytus* Holbrook, 1842; *Ctenosaura* Wiegmann, 1828; *Dipsosaurus* Hallowell, 1854; *Enyaliosaurus* Gray, 1845; *Holbrookia* Girard, 1851; *Iguana* Laurenti, 1768; *Phrynosoma* Wiegmann, 1828; *Sator* Dickerson, 1919; *Sauromalus* Duméril, 1856; *Sceloporus* Wiegmann, 1828; *Uma* Baird, 1858; *Uta* Baird & Girard, 1852. According to Mittleman's system there were two main evolutionary lines represented in this group, both stocks being derived from the genus *Ctenosaura*. One line was composed of the relatively primitive genera *Dipsosaurus* and *Sauromalus* (and presumably *Enyaliosaurus* and *Iguana*) and the more highly specialized *Callisaurus, Holbrookia, Uma* and *Crotaphytus*. Also placed in this section were two of the component genera, *Petrosaurus* and *Streptosaurus*, removed from *Uta* by Mittleman. These two genera were supposed to be derived from *Crotaphytus*. The second major stock included *Phrynosoma, Sceloporus, Sator, Urosaurus* and *Uta*. The last three genera were considered by Mittleman to be independent derivatives of *Sceloporus*.

Stejneger & Barbour (1943) and Smith & Taylor (1950), in their checklists of the lizards of the United States and Mexico, adopted Mittleman's arrangement of the "utas," while Smith (1946, p. 92) presented a somewhat modified phylogeny of North American iguanids that is nevertheless in basic agreement with Mittleman's work. Many herpetologists, some perhaps influenced by the above acceptance of Mittleman's nomenclature, have followed his conclusions. On the other hand, other workers have been inclined to follow Oliver (1943, p. 106), who was loathe to recognize Mittleman's genera because so few characters separate them, and have retained all the species within a single genus. Schmidt (1953) and Stebbins (1954), among others, adhered to the latter view.

It is obvious from the above discussion that Mittleman's classification hinges more upon his

interpretation of the phylogeny of the North American iguanids than upon marked structural differences between the several species groups. If his conception of the evolution of these lizards is correct, it would appear that recognition of four genera of "utas" is necessary. If, however, his interpretation of the group's phylogeny is erroneous and no additional morphologic features can be discovered to support his divisions, Oliver's conclusion that but one generic unit is involved must be accepted. The problem, therefore, is: (1) to determine if any characteristics will separate the groups included in the genus *Uta* prior to Mittleman's study and (2) to evaluate the relationships between these groups and other iguanid genera.

Plan of Analysis

My interest in this problem was originally aroused during preliminary examination of skeletal material being assembled for studies on the Iguanidae. At that time it was noted that there were remarkable differences between several species of *Uta* (*sensu latu*) in the nature of the sternum and associated structures. If these differences proved to be constant for each species group, it was thought that they might validate generic segregation. Consequently, since the external features used to distinguish between the several groups of "utas" were of doubtful significance, the present analysis has centered around a review of their comparative osteologies. A survey of external differences has also been undertaken in order to determine if these substantiate differences in internal characteristics.

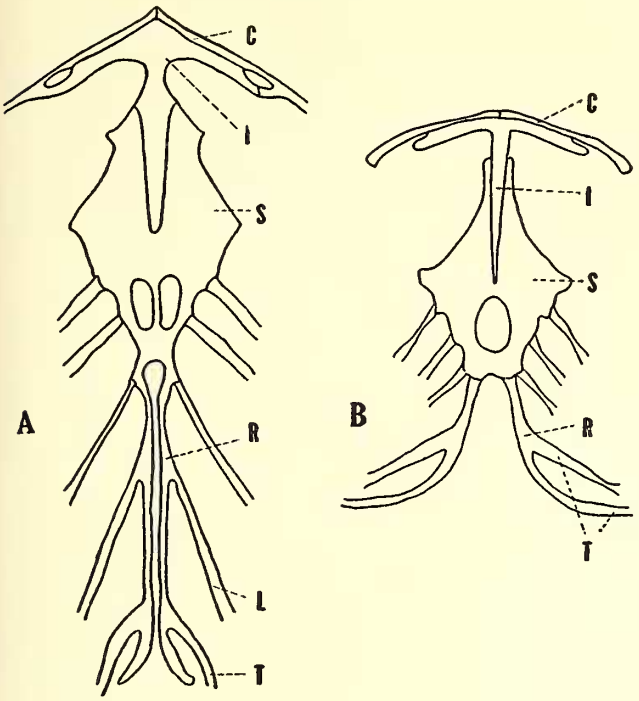
It became apparent early in the study that the principal difficulties of the problem lay in the allocation of the genera *Urosaurus* and *Uta*. Once these genera had been properly placed, the position of *Petrosaurus* and *Streptosaurus* can be readily understood. For this reason, a comparison of *Urosaurus* and *Uta* forms the first part of this report. The second section deals with the status of *Petrosaurus* and *Streptosaurus*. A third section considers a recent attempt to classify these lizards on the basis of ecologic characteristics. The final portion of the paper is concerned with the general relationships between the "utas" and other iguanid lizards.

Information for this report has been derived from preserved material of all genera and species mentioned. In addition skeletons of the following species, prepared by the Bolin Method (Bolin, 1936), have been examined: *Callisaurus draconoides* (4), *Crotaphytus collaris* (1), *Crotaphytus wislizeni* (2), *Ctenosaura hemilopha* (1), *Dipsosaurus dorsalis* (3), *Phrynosoma coronatum* (4), *Phrynosoma platyrhinos* (1), *Sator angustus* (2), *Sator grandaevus* (2), *Sauromalus ater* (1), *Sauromalus obesus* (1), *Sceloporus magister* (5), *Sceloporus occidentalis* (10), *Sceloporus orcutti* (1), *Uma notata* (1), *Urosaurus graciosus* (2), *Uta mearnsi* (1), *Uta slevini* (1), *Uta stansburiana* (5). Also available was additional skeletal material or cleared and stained specimens of: *Amblyrhynchus cristatus* (5), *Anolis garmani* (2), *Anolis leucophaeus* (1), *Brachylophus fasciatus* (1), *Conolophus pallidus* (1), *Conolophus subcristatus* (10), *Ctenosaura acanthura* (1), *Ctenosaura pectinata* (2), *Ctenosaura similis* (3), *Cyclura carinata* (1), *Cyclura cornuta* (3), *Cyclura stejnegeri* (1), *Holbrookia maculata* (1), *Holbrookia texana* (1), *Iguana iguana* (15), *Leiocephalus psammodromus* (2), *Sauromalus hispidus* (1), *Sauromalus varius* (1), *Uma inornata* (1), *Uma scoparia* (1), *Urosaurus auriculatus* (1), *Urosaurus bicarinatus* (1), *Urosaurus nigricaudus* (1), *Urosaurus ornatus* (1) and *Uta thalassina* (2). The pertinent morphological points have been uncovered by dissection on specimens of *Enyaliosaurus quinquecarinatus, Urosaurus microscutatus* and representatives of most of the major subpopulations of *Uta stansburiana* and its insular allies.

Comparison of *Urosaurus* and *Uta*

Mittleman (1942, pp. 109-112) presented what purport to be extensive differential diagnoses of *Petrosaurus, Streptosaurus, Urosaurus* and *Uta*. Oliver (1943, p. 106) pointed out that few of the listed features satisfactorily distinguished between these groups and that none of them clearly indicated the existence of more than one genus. Mittleman (1942, p. 106) stated that there were no differences in the bony structures of these lizards that would separate them from one another or from *Sator* and *Sceloporus*. Preliminary examination of skeletal material tended to dispute this latter assertion and my study has been aimed at discerning whether osteological features distinguished the nominal groups of "utas."

The lizards placed in the genera *Urosaurus* and *Uta* resemble one another rather closely in the structure of the skull, vertebral column, girdles and limbs. The two groups are profoundly divergent, however, in the condition of the sternal plate and associated structures. These differences, supported to some extent by external structures, convince me that two genera can be recognized. The differences between *Urosaurus* and *Uta* in sternal anatomy are summarized as follows:



TEXT-FIG. 1. Sternal plates and associated structures in iguanid lizards from ventral view. **A.** Diagram of urosaurine sternum from specimen of *Urosaurus graciosus*. **B.** Diagram of utiform sternum from example of *Uta stansburiana*. Abbreviations denote the following structures: **C.** clavicle; **I.** interclavicle; **S.** sternal plate; **R.** xiphisternal rod; **L.** lateral xiphisternal rib; **T.** terminal xiphisternal rib.

Urosaurus.—Sternal plate rather long and relatively narrow, with the posterior margin tapering almost to a point; xiphisternal rods originating near center line of sternal plate, long, being much longer, when measured from the sternal plate to origin of terminal xiphisternal ribs, than sternal plate is wide; lateral xiphisternal ribs present.

Uta.—Sternal plate relatively short and broad, with the posterior margin truncate and forming a wide base; xiphisternal rods originating at lateral edges of posterior margin of sternal plate, short, being much shorter, when measured from sternal plate to origin of terminal xiphisternal ribs, than sternal plate is wide; no lateral xiphisternal ribs, only terminal ones.

These sternal characteristics have been observed in osteological material of the generic types, *Urosaurus graciosus* Hallowell, 1854, and *Uta stansburiana* Baird & Girard, 1852, and verified in examples of all major groups within these nominal genera. Text-fig. 1 illustrates the sternum in these groups. The apparent differences in the nature of the interclavicle-clavicle relationships shown in these figures are not constant throughout the two groups. Elsewhere in the family Iguanidae the shape and relative position of these elements are frequently of value in generic determination.

The condition of the sternum has not previously been employed to characterize genera of the Iguanidae and some question may arise as to the validity of a distinction made upon this feature. Conceivably, the observed differences could be due to modifications of a single sternal type within a single genus. To confirm the generic significance of the sternal condition, an examination of this structure was made on examples of the majority of North American iguanids, exclusive of the myriad forms within the genus *Sceloporus*. This examination revealed that not only is the type of sternum consistent within every genus but that the condition of the structure appears to have considerable phylogenetic significance. Although the sternal plates and associated structures of some other American iguanids superficially resemble the condition found in *Uta*, within the section of the family closely allied to *Urosaurus* and *Uta* the sternum seems indicative of two evolutionary lines. In this regard, the distribution of the two sternal types in this section of the Iguanidae is informative:

Urosaurine	Utiform
Sator	*Callisaurus*
Sceloporus	*Holbrookia*
Urosaurus	*Phrynosoma*
	Uma
	Uta

In the material examined, the typical uro-

saurine sternum in found only in the three genera listed above, although some *Sceloporus* tend to have rather short xiphisternal rods. These groups have usually been held by previous workers to be closely allied on the basis of external features, and the sternal arrangement fully supports this view. It seems likely that *Urosaurus* is best understood as a specialized off-shoot of *Sceloporus* from which it differs primarily in the presence of a fully developed gular fold and the absence of a scapular foramen, no gular fold but a scapular foramen being present in *Sceloporus*. *Uta* appears to be a specialized genus related to the highly adapted, but apparently more primitive, *Callisaurus-Holbrookia-Uma* series. *Uta* is probably best considered as a recent derivative of this stock and as such can only be distantly allied to *Urosaurus*, which it resembles in several external features. In view of the evidence of complete morphological separation and the probability of different origins it would seem that *Urosaurus* and *Uta* ought to be retained as distinct genera.

Because the principal characteristics diagnostic of the genera *Urosaurus* and *Uta* are internal ones, it seemed worthwhile to attempt to determine if there were any external features that distinguish them. Such characters might be useful for rapid identification or in artificial keys. Careful examination of examples of all the species groups within the two genera reveals that a single scutellational character can be used for generic recognition. This feature involves the arrangement of the scales in the nasal region and makes it necessary to digress at this point from the major problem of the paper to treat a matter of terminology.

Unfortunately herpetologists have seldom attempted to standardize the nomenclature of the head scales in lizards. General agreement has been reached in dealing with the comparatively simple arrangement of snakes, but since the size, shape and position of the scales vary from lizard group to lizard group, the subject has become surprisingly complex. In the case in point, for example, Smith (1946, p. 276) and Mittleman (1942, p. 123), in naming the head scales of *Urosaurus* and *Uta*, use entirely different terms for what appear to be positionally homologous units. It is understandable under these circumstances why previous workers have overlooked scale characters that readily separate these two genera. Because of the great diversity in the number and disposition of head scales in different lizard families, it does not seem possible or desirable to instigate a universally applicable nomenclature. Nevertheless, it does seem worthwhile to employ a standard set of terms within familial or subfamilial limits. While this cannot be accomplished as yet with the iguanids because of our lack of understanding of the suprageneric groupings within the family, I have attempted to standardize the scale nomenclature for the nasal region in the genera allied to *Urosaurus* and *Uta*. Subsequent work will probably find that this system can be applied without too much difficulty to more distantly related and less specialized genera.

Terminology for Scales in Nasal Region

Rostral.—Scale at tip of snout, bordering upper lip.

Internasals.—Usually a double pair (anterior and posterior) of scales lying between the nasals on top of the snout.

Nasals.—Scales in which the nostrils are pierced.

Postrostrals.—These are the subnasals of *Urosaurus* as defined by Mittleman (1942) and the postrostrals of *Uta* and *Sceloporus* according to Smith (1946); the two series are homologous in position, bordering the nasal along its anterior and lower margins and on occasion separating the rostral from the anterior internasals.

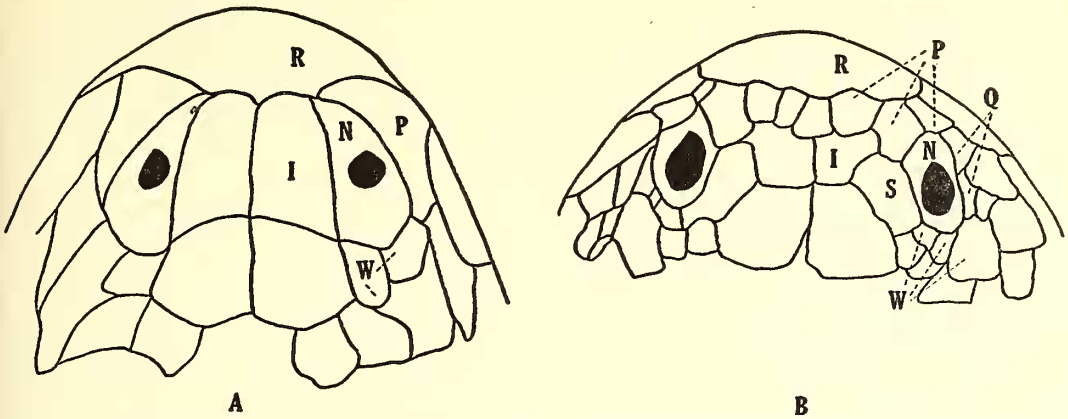
Supranasals.—Scales bordering the upper margins of the nasals and separating the nasals from the internasals.

Subnasals.—Scales bordering the lower edge of the nasals and lying posterior to the postrostrals; they separate the nasals from the supralabials.

Postnasals.—Scales bordering the posterior margin of the nasals and separating them from the loreals or canthals.

The set of terms here defined and figured (Text-fig. 2) can be applied to the scales in the nasal region of the following genera (names as listed by Mittleman): *Petrosaurus, Sator, Sceloporus, Streptosaurus, Urosaurus* and *Uta*. The system is not satisfactory when working with genera with a more or less homogenous complement of head scales as in *Crotaphytus, Ctenosaura, Dipsosaurus, Enyaliosaurus, Iguana* and *Sauromalus*. *Callisaurus, Holbrookia, Phrynosoma* and *Uma* have the head scales somewhat intermediate between the *Urosaurus-Uta* group and the *Iguana*-like lizards. There is probably little need to distinguish between the scales in the nasal region at such a fine level as is profitable in *Urosaurus* and *Uta* in this *Phrynosoma-Holbrookia* line.

The genera *Urosaurus* and *Uta* are distinguished by: *Urosaurus* having the nasals and internasals in contact and lacking supranasals



TEXT-FIG. 2. Scutellation of nasal region in iguanid lizards. **A.** Dorsal view of snout of *Urosaurus*. **B.** Dorsal view of snout of *Uta*. The following symbols indicate the pertinent scales: **I.** internasal; **N.** nasal; **P.** postrostral; **Q.** subnasal; **R.** rostral; **S.** supranasal; **W.** postnasal.

(Text-fig. 2,A); *Uta* has the anterior internasals separated from the nasals by definite supranasal scales (Text-fig. 2,B). Although *Urosaurus* is distinct from members of the *Uta stansburiana* group in having two distinct abdominal patches in the adult males and sometimes in the female and never any axillary or shoulder dark spots (in *Uta stansburiana* and its allies no well-defined abdominal patches of color are present in either sex, although the belly may be suffused with blue, gray or black in adult males and there is usually a dark blue or black axillary spot and frequently a dark spot anterior to the shoulder insertion), these differences break down when other members of the genus *Uta* are considered.

In *Urosaurus* and *Uta* the rostral scale may or may not be in contact with the internasals. If the rostral and internasals are separated the postrostrals lie between them. This arrangement appears to be quite variable in populations of *Uta* but it is more consistent within specific limits in *Urosaurus*. In my material usually 90 per cent. or more of the specimens of a single form have the same internasal-rostral relationship. In *Urosaurus bicarinatus* (A. Duméril, 1856), not all subspecies seen, *Urosaurus nigricaudus* (Cope, 1864) and *Urosaurus microscutatus* (Van Denburgh, 1894), the rostral usually meets the anterior internasals. *Urosaurus auriculatus* (Cope, 1871), *Urosaurus graciosus* Hallowell, 1854, and *Urosaurus ornatus* (Baird & Girard, 1852), not all subspecies seen, usually have the postrostrals preventing a contact between the rostral and internasals.

In related genera these external features are variable. *Sator* has supranasals and definite abdominal color patches in adult males. Supranasals may be present or absent in *Sceloporus* although apparently consistently present or absent within species limits, and the abdominal color patches are regularly present in many species in adult males and sometimes in females. In several species these color patches are totally absent. As previously indicated, the scales in the nasal region of *Callisaurus, Holbrookia, Phrynosoma* and *Uma* are relatively small and cannot be recognized as definite postrostrals, supranasals or internasals. Definite abdominal color patches are present in males (and sometimes in females) of all these genera except *Phrynosoma*.

THE STATUS OF *Petrosaurus* AND *Streptosaurus*

Since *Urosaurus* and *Uta* have been shown to be distinct, the position of *Petrosaurus* and *Streptosaurus*, two nominal genera formerly included in *Uta*, can now be analyzed. According to Mittleman, *Petrosaurus* was derived from *Crotaphytus* and *Streptosaurus* from *Petrosaurus*. There can be no question regarding the close relationship of *Petrosaurus* and *Streptosaurus* but their supposed affinity to *Crotaphytus* is, on the basis of data accumulated in the preparation of this report, subject to considerable doubt. Evidence showing why *Petrosaurus* and *Streptosaurus* cannot be closely related to *Crotaphytus* will be presented later in this paper.

The first problem at hand is to determine the generic status and differences between *Petrosaurus thalassinus* (Cope, 1863) and the doubtfully valid form *Petrosaurus reprens* (Van Denburgh, 1895) on the one hand and the two nominal species of *Streptosaurus, mearnsi* (Stejneger, 1894) and *slevini* (Van Denburgh, 1922) on the other. Mittleman (1942, pp. 110-111) attempted to segregate these two species-groups

on the basis of numerous characters. Many of the features listed by him were given under both genera, however, and an analysis of the others indicates that few of the differences hold. The features employed by Mittleman are given below:

Petrosaurus	*Streptosaurus*
1. Larger ventrals	1. Smaller ventrals
2. Enlarged, strongly keeled caudal scales	2. Caudals weakly keeled
3. Three rows of enlarged supraoculars	3. Two rows of enlarged supraoculars
4. Anterior gular fold (pregular) well-developed	4. Anterior gular fold poorly developed
5. Lateral fold poorly developed	5. Lateral fold well-developed
6. Dorsal pattern of bands, no neck ring	6. Dorsal pattern without bands, a neck ring
7. No abdominal color patches	7. Abdominal color patches in males
8. No palatine bones	8. Palatine bones present

These features are considered in the order given above. (1) There appears to be a definite difference in the size of the ventral scales in the two groups but this character is of questionable generic significance. (2) The differences in the degree of keeling of the caudal scales are evident but hardly generic in character. (3) The number of rows of enlarged supraoculars is a consistent feature. (4) The condition of the pregular fold in life is variable and the degree to which it appears to be developed in preserved material is not consistent within any available sample. This character is therefore useless for distinguishing between the two groups. (5) The same remarks given for the pregular fold apply to the condition of the lateral fold. (6) The dorsal bands and nuchal collar are present in both *Petrosaurus* and *Streptosaurus* but differ in degree of intensity. The dark nuchal collar of *Streptosaurus* appears to be the same pattern element as the anterior dorsal band in *Petrosaurus*. The posterior bands are prominent in the latter genus but, although present in the former group, they are obscured to some extent by the darker body coloration. (7) Both groups have the same type of abdominal coloration in adult males although the predominant color in both living and preserved material is blue in *Streptosaurus* and blackish in *Petrosaurus*. These colored areas appear to constitute definite abdominal patches although the color tends to suffuse over the entire ventral surface. Laterally the suffusion of darker color is similar to the condition found in adult male *Uta stansburiana;* however, this latter group does not have extensive coloration superimposed on the ventral abdominal surfaces. (8) A palatine bone is present on both sides of the skull in all specimens of either group seen by me, although the bone is somewhat thinner than in less specialized iguanids.

It is obvious that the two presumed genera are distinct from one another in a few minor details of scutellation and coloration and that none of the observed differences seem indicative of two distinct generic groups. Examination of skeletal material of the several species shows that they are essentially similar. The only points of difference between them are in the relative proportions of a few elements. Because of the absence of trenchant distinguishing features and the fact that all workers, including Mittleman, have considered these taxa to be closely related, inclusion of these lizards in a single genus seems appropriate. Fully supporting this conclusion are the facts of morphology and the distributional pattern of the several species. The form *mearnsi* has a range from Riverside County, California, south in Baja California, Mexico, to the region of Santa Rosalia. *Thalassina* occupies the southern portion of the peninsula from Comundú (about 75 miles south of Santa Rosalia) southward. If the form *reprens* is recognized, it would occupy the northern portion of the range given for *thalassina*. Although additional evidence is needed to verify this point, it is likely that *thalassina* is more primitive than *mearnsi*. The insular form, *slevini*, is obviously of close affinity with *mearnsi*. It is restricted to Isla Angel de la Guarda and adjacent islets in the Gulf of California.

The question now arises as to the generic placement of these three species. Since the pectoral apparatus as well as the scutellation and general morphology of these forms are of the utiform type, the genera allied to *Sceloporus* need not be considered. The condition of the vertebrae, the nasal structure, the scapulocoracoid foramina (Text-fig. 5) and the sternum of these three forms are totally different from these features in *Crotaphytus* and its relatives. Consequently these genera also need not be discussed. (See the section on classification at the end of this paper for additional information on the affinity between these species and *Crotaphytus* postulated by Mittleman). These eliminations leave only the genera associated with *Uta* as possible congenitors of *mearnsi, slevini* and *thalassina*. Within this series, only *Uta* approaches the three in osteological and other morphological features and it is here that the relationship apparently lies. The following summary of characteristics

will separate *Uta stansburiana* and its allies from the giant Baja California forms:

Uta: enlarged supraoculars in a single series; well-defined median and lateral frontonasal scales; scales along gular fold much larger than gulars; no definite dorsal bands, no nuchal collar; neural spines well-developed, higher than long; usually three sternal ribs (rarely four).

Petrosaurus: enlarged supraoculars in two or three series; no definite median and lateral frontonasals; scales along gular fold same size as gulars; back with definite dark bands, a nuchal dark collar; neural spines low, longer than high; four sternal ribs.

The differences between *Uta* and *Petrosaurus* are slight and no single feature in itself is particularly significant. However, the total character-complements of the two groups are rather divergent and a decision as to the most propitious allocation of the species involved is difficult. Although there is considerable merit in recognizing *Petrosaurus* as a phylogenetic line distinct from *Uta,* the obvious close relationship between the two and the kind of differences separating them lead me to conclude that the evolutionary picture can best be explained by placing them in a single genus. Recognition of two subgeneric categories within the genus *Uta,* one for *stansburiana* and its immediate allies and a second (*Petrosaurus*) for the *mearnsi* group, may be a useful way to emphasize the differences between the two evolutionary lines in the genus.

In this regard it should be noted that the shoulder spot of *Uta stansburiana* and related forms appears to represent the remnant of the nuchal collar of *Uta mearnsi, Uta slevini* and *Uta thalassina.* In these latter forms, the dark blue or black lateral and abdominal suffusions of the male are most intensive in the axillary region, and the axillary spot in the *Uta stansburiana* section is probably a retention of the anterior portion of this densely pigmented area.

The Ecologic Genus and the Present Problem

The concept of the genus adopted in the present report agrees in principle with that given by Mayr (1942, pp. 282-286). Because of the nature of the material studied, the degrees of relationship and difference between the several groups are based upon morphologic characteristics, although it is clearly understood that other kinds of characters may be used, and ought to be used when available, in generic definition. The genera accepted in this account are therefore convenient but natural groupings of species separated from other such units by discontinuities in morphologic variation.

A radical conception of the genus in terms of ecology has recently been adopted by one herpetologist (Lowe, 1955a; 1955b) and applied to the problem of the generic status of *Uta* and its allies. Lowe holds the extreme position that genera can be recognized on the basis of ecologic divergence alone, without support from any other kind of characteristics. The difficulties arising from the rigid application of this idea are too numerous to consider at this time, but may be summed up as follows: (1) any two species, if different from each other in ecology, regardless of similarities in morphology, physiology or other features, may be recognized as distinct genera; (2) all species having the same or very similar ecologies, regardless of genetic relationships or differences in other features, may be placed in the same genus.

Lowe and Norris (in Lowe, 1955a) utilized this concept as the basis for a classification of the lizards formerly placed in the genus *Uta.* They maintained Mittleman's arrangement of these species because of supposed differences between and similarities within the groups involved. According to these authors the species can be arranged as follows:

Genus *Petrosaurus*
  Subgenus *Petrosaurus*
  Subgenus *Streptosaurus*
Genus *Urosaurus*
Genus *Uta*

Petrosaurus and *Streptosaurus* were placed together because of their cliff-dwelling propensities. *Urosaurus* was retained as a distinct genus because the species within the group are, according to Lowe and Norris, plant-dwellers and plant-climbers. *Uta* is supposedly distinguished from the other two genera by living on the ground. The genera are thus recognized because they occupy different ecologic niches.

The primary reason why Mittleman's classification of these lizards has not been generally accepted lies in his failure to present convincing evidence that the several groups were morphologically different from one another. The most striking morphologic feature listed by him as separating *Uta* and *Urosaurus,* for example, was the homogeneous dorsal scutellation of the former and the differentiation of the paravertebral scales in the latter. This character fails to hold for *Urosaurus microscutatus* and some examples of *Urosaurus nigricaudus* which have a homogeneous complement of dorsal scales.

The system adopted by Lowe and Norris can only have merit if it is based upon consistent ecologic features that do not vary within the several groups established by Mittleman.

Unfortunately this is not the case. Firstly, several species placed within the nominal genera do not have the ecologic mode of life attributed to them by Lowe and Norris. *Urosaurus microscutatus* and *Urosaurus nigricaudus* are typically found on rocks and boulders, often in association with *Uta* (*Petrosaurus*) *mearnsi* or *Uta* (*Petrosaurus*) *thalassina* and only rarely in bushes or other plants. Secondly, there is considerable variation in the habitats occupied by different individuals or populations within many species. The supposedly ground-living *Uta stansburiana* is frequently found in low bushes or on rocks or boulders. Many of the insular forms of *Uta* are more or less restricted to this latter habitat. It may be assumed that the species in the other generic groups also exhibit some variation in habitat selection. Finally, it ought to be pointed out that members of the related genera *Sator* and *Sceloporus* are found in all three habitats attributed to *Petrosaurus, Urosaurus* and *Uta.* Within the limits of *Sceloporus,* various species tend to be inhabitants of trees and bushes, or are typically found on the ground or in rocky and boulder regions. Other members of this genus may occur in two or three of these habitats. The two species of *Sator* are unselective in habit, individuals of the same form being commonly found in all three situations. If ecologic characteristics alone were used in setting up the genera in this section of the Iguanidae, all of the taxa mentioned above would have to be placed in a single genus since no clear-cut distinction can be made between them. If all other characters were disregarded, it would be possible to re-align the species into several genera on the basis of habitat preference, but genera erected on this criterion would be extremely artificial. Either of these alternatives, particularly in the light of the morphologic data presented in this report, illustrates the tangles that ensue from application of a strictly ecological concept of the genus.

The statement by Lowe and Norris (apparently based upon their evaluation of ecologic features) that *Petrosaurus* is not closely related to either *Crotaphytus* (as postulated by Mittleman) or to *Uta,* needs no further comment here.

Remarks on the Classification of North American Iguanids

The principal argument advanced by Mittleman (1942) for the division of the genus *Uta* into four genera was his idea of the phylogeny of the several species groups. His system of classification was based upon the assumption that the North American iguanids form a natural group of genera and that this stock includes two related but divergent evolutionary lines. Mittleman suggested that the genus *Ctenosaura* represents the primitive ancestor from which both lines evolved. One of these stocks contained the genera (in approximate order from primitive to advanced) *Dipsosaurus, Sauromalus, Callisaurus, Holbrookia, Uma, Crotaphytus* and the nominal genera *Petrosaurus* and *Streptosaurus.* The other group included *Phrynosoma, Sceloporus, Sator, Urosaurus* and *Uta.* Smith (1946, p. 92) retained Mittleman's basic arrangement but added *Leiocephalus* Gray, 1827, to the *Phrynosoma-Uta* line.

In the preceding sections of this report, information is presented to substantiate Mittleman's concept of *Urosaurus* and *Sator* as allies of *Sceloporus.* However, all other data accumulated during an investigation of this problem are in strong contradiction to Mittleman's and Smith's basic classification of northern iguanids. Evidence at hand clearly indicates that the consideration of the North American iguanids as a natural inter-related group is without factual foundation. Because my views are in sharp contrast to those of Mittleman it has been necessary to present a summary of tentative conclusions regarding the relationships of these lizards. Conclusions are based upon available information in the literature (especially Boulenger, 1885; Cope, 1900; Camp, 1923) and on a preliminary evaluation of skeletal and other morphological features. The classification outlined is therefore a tentative one to be modified in its details by later work. The main lines of evolution, however, appear to be clearly recognizible, and it is hoped that my arrangement will stand scrutiny better than that proposed by Mittleman.

Insofar as can be determined at this time, the so-called Nearctic iguanids form two diverse groups that can be only distantly related. These two sections are distinguished by marked differences in vertebral and nasal structures and include several genera not usually recognized as being allied to Nearctic forms. No species intermediate in significant characters has been found to bridge the gap between the two lines. Since a thorough revision of the entire family would be necessary to establish the exact status of the suprageneric groups, no attempt has been made to place them in a definite classificatory category.

One of the primary divisions in the Iguanidae, represented by a number of genera in North America, is a stock characterized as follows:

Vertebrae: each dorsal vertebra provided with zygosphenes and zygantra in addition to the zygapophyses.

Nasal structure: nasal organ of the relatively simple S-shaped type, concha present *(Dipsosaurus*-type of Stebbins, 1948, p. 209).

This section, hereafter referred to as the iguanine group, includes the following genera:

Amblyrhynchus Bell, 1825
Brachylophus Cuvier, 1829
Conolophus Fitzinger, 1843
Crotaphytus Holbrook, 1842
Ctenosaura Wiegmann, 1828
Cyclura Harlan, 1824
Dipsosaurus Hallowell, 1854
Enyaliosaurus Gray, 1845
Iguana Laurenti, 1768
Sauromalus Duméril, 1856

Although I have not been able to examine the nasal structure of *Amblyrhynchus, Brachylophus, Conolophus* and *Cyclura,* these genera have the typical iguanine vertebrae with zygosphenes and zygantra. Their agreement with other members of the group in this regard and their close similarity in basic features make it probable that they possess S-shaped nasal organs. Additional genera may be added to this section when their skeletons and nasal structures have been studied.

The second group, essentially North American in distribution, is characterized by:

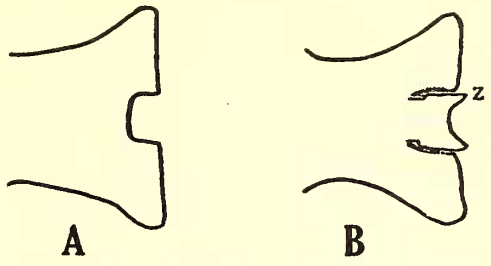
Vertebrae: dorsal vertebrae without zygosphenes and zygantra.

Nasal structure: nasal organs of the sink-trap type, no concha (*Uma*-type of Stebbins, 1948, p. 205).

This section, hereafter called the sceloporine line, contains:

Callisaurus Blainville, 1835
Holbrookia Girard, 1851
Phrynosoma Wiegmann, 1828
Sator Dickerson, 1919
Sceloporus Wiegmann, 1828
Uma Baird, 1858
Urosaurus Hallowell, 1854
Uta Baird & Girard, 1852

Illustrations of the differences in vertebral and nasal structure are given in Text-figs. 3 & 4. It should be noted that in some species of *Phrynosoma* and *Sceloporus,* a vertical facet is present on each side of the neural lamina at the anterior end of the vertebrae in the same position where



TEXT-FIG. 3. Anterior portion of dorsal region of vertebrae in iguanid lizards. **A.** Diagram of sceloporine vertebra of *Uta mearnsi.* **B.** Diagram of iguanine vertebra of *Crotophytus wislizeni.* The letter **Z** lies adjacent to one of the zygosphenes.

zygosphenes are developed in iguanine lizards. There are no zygantra in species with these facets, and the latter structures do not appear to be morphologically similar to true zygosphenes, which are horizontally flattened and markedly projected anteriorly from the base of the neural spine.

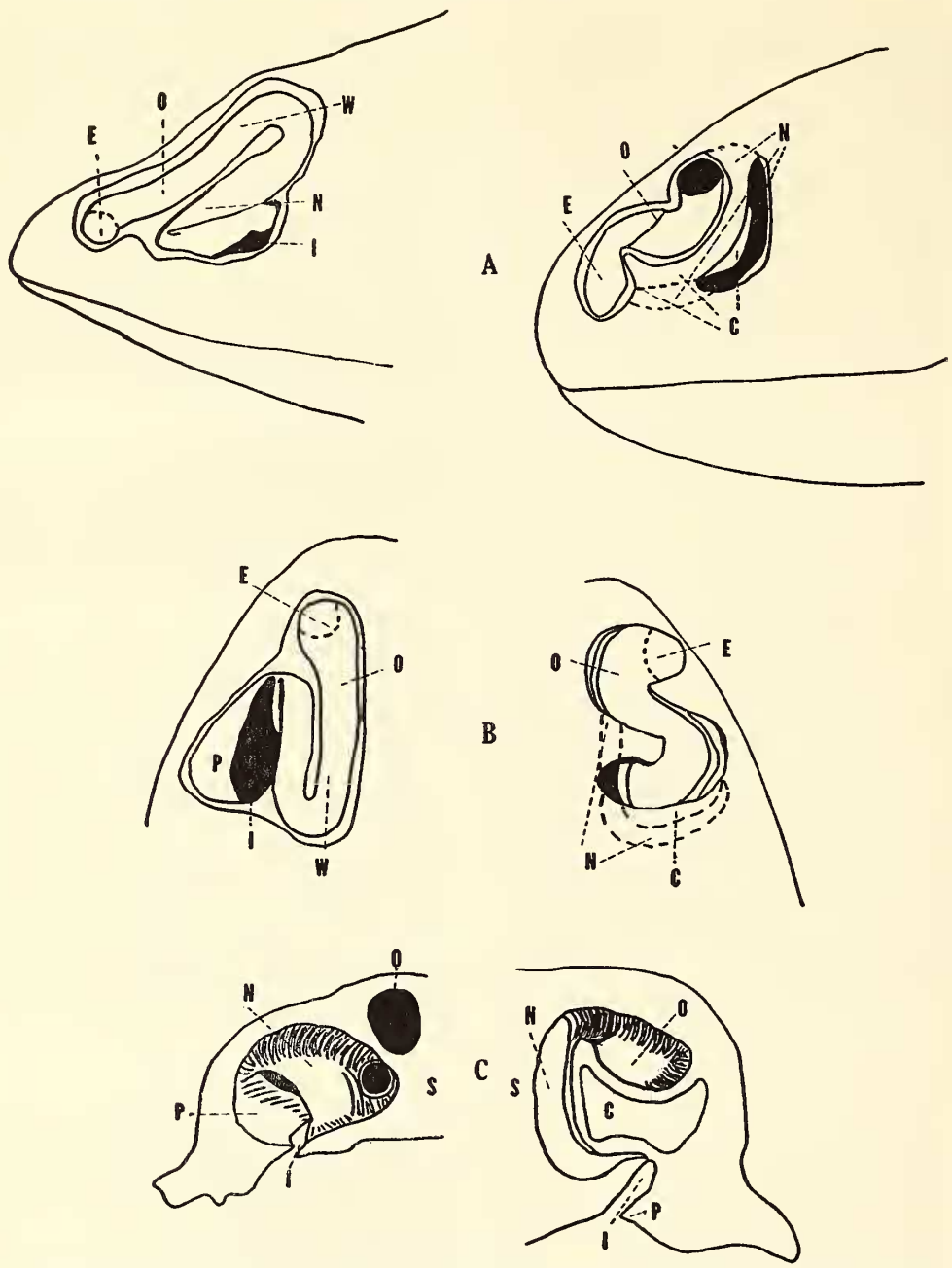
In addition to the primary differences listed above, the two groups differ from one another in several general tendencies that hold for a majority of genera.

Iguanine line.—Teeth usually on pterygoid (usually on palatine as well in *Crotaphytus wislizeni*); the small parietal foramen usually pierced in frontal or in suture between frontal and parietal bones; parietal bone thick; pectoral girdle usually with primary and secondary coracoid foramina, scapular and scapulocoracoid foramina also present (Text-fig. 5); head scutellation essentially a homogenous group of small scales not arranged into definite series; interparietal scale small, not markedly larger than adjacent head scales; usually a mid-dorsal crest of enlarged scales.

Sceloporine line.—Never any palatal teeth; usually a large parietal foramen pierced in a thin membraneous parietal bone; never any secondary coracoid foramen in pectoral girdle, scapular foramen often absent (Text-fig. 5); head scutellation usually a heterogeneous mixture of enlarged and smaller scales arranged in definite series; interparietal scale usually enlarged, much larger than adjacent scales; never a mid-dorsal crest of enlarged scales, although paravertebral scales may form an enlarged series.

Table 1 indicates the distribution of these features in the individual genera.

The evolutionary significance of the development of the specialized vertebrae with zygosphenes and zygantra and the divergent types of nasal structure are not certainly known. The



TEXT-FIG. 4. Structure of nasal organs in iguanid lizards. **A.** Lateral view. **B.** Dorsal view. **C.** Cross-sectional view. Figures on the left of the sink-trap nasal organization of *Callisaurus draconoides* typical of the sceloporine line. Figures on right of the S-shaped nasal organization of *Dipsosaurus dorsalis* typical of the iguanine line. Abbreviations indicate the most important parts as follows: **C.** concha; **E.** external naris; **I.** internal naris; **N.** nasal cavity; **O.** vestibule; **P.** palatine fold; **S.** nasal septum; **W.** nasal passage. All figures after Stebbins (1948).

vertebral modification which provides for two additional points of contact and support between vertebrae probably has something to do with the large size attained by most iguanine lizards. The zygantra are significantly reduced in size in *Crotaphytus,* the genus including the species having the smallest adult size within the section. Stebbins (1948, p. 213), the original discoverer

of the differences in nasal structure, has considered at length the possible functional significance of the sink-trap nasal arrangement. He concludes that this feature is an evolutionary adaptation to intensification of the problem of cleansing inspired air in arid enviroments and under circumstances where the lizard buries itself in the soil. The S-shaped nasal structure of the iguanine line is interpreted by Stebbins to represent a somewhat specialized stage intermediate in its adaptation for an arid enviroment between the relatively unmodified structures of other lizards and the complex condition in the sceloporines.

The genus *Leiocephalus* suggested by Smith (1946, p. 92) as a possible ally of *Sceloporus* has an unmodified nasal organization totally unlike that found in either the iguanines or sceloporines. *Leiocephalus* does not appear to be particularly closely related to any of the genera considered in this report.

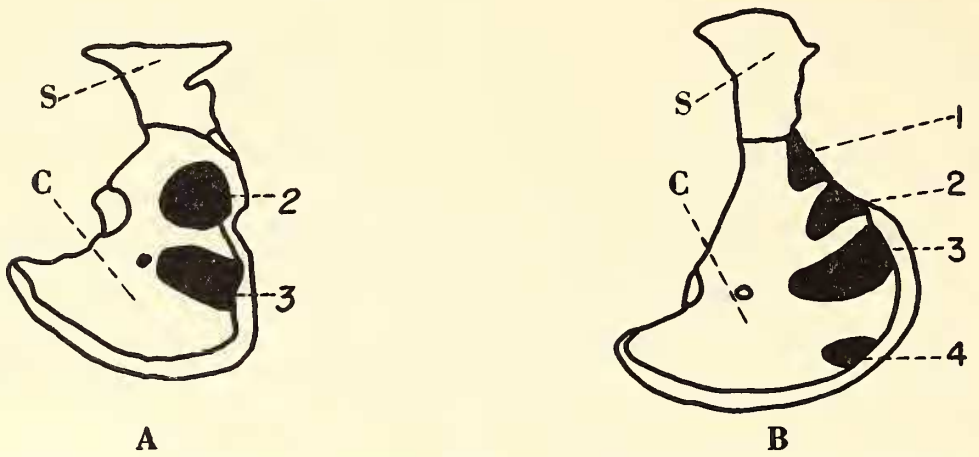
It does not seem advisable at present to speculate on the relationships of the iguanine lizards, due to lack of adequate material. Final decisions on the phylogeny of the sceloporine section must also await additional research. However, a tentative scheme of relationships within the latter group has been drawn up and is presented in Text-fig. 6.

TABLE 1. CHARACTERISTICS OF IGUANINE AND SCELOPORINE LIZARDS[1]

Group	Pterygoid Teeth	Parietal	Parietal Foramen	Pectoral Foramina S	S-C	C	C′	Head Scales	Inter-Parietal Scale	Mid-Dorsal Crest
Iguanines:										
Amblyrhynchus	+ (B)	T	sm. F or F-P	X	X	X	X	H	sm.	+
Brachylophus	+	T	sm. F or F-P	–	–	–	–	H	sm.	+
Conolophus	+ (B)	T	sm. F or F-P	X	X	X	X	H	sm.	+
Crotaphytus	+	T	sm. F or F-P	X	X	X	X	H	sm.	–
Ctenosaura	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
Cyclura	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
Dipsosaurus	+ (B)	T	sm. F	X	X	X	O	H	sm.	+
Enyaliosaurus	+	T	.....	–	–	–	–	H	sm.	+
Iguana	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
Sauromalus	+	T	sm. F or F-P	X	X	X	X	H	sm.	–
Sceloporines:										
Callisaurus	–	t	l. P	X	X	X	O	h	l.	–
Holbrookia	–	t	l. P	X	X	X	O	h	l.	–
Phrynosoma	–	T	sm. F-P	X	X	X	O	H	l.-sm.	–
Sator	–	t	l. P	O	X	X	O	h	l.	–
Sceloporus	–	t	l. P	X	X	X	O	h	l.	–
Uma	–	t	l. P	X	X	X	O	h	l.	–
Urosaursus	–	t	l. P	O	X	X	O	h	l.	–
Uta	–	t	l. P	O	X	X	O	h	l.	–

[1] The following list indicates the meaning of the symbols utilized in the table:

+ = present
– = absent
(B) = according to Boulenger (1883)
T = thickened
t = thinned
sm. = small
l. = large
F = frontal bone
P = parietal bone
F-P = suture between frontal and parietal bones
S = scapular
S-C = scapulocoracoid
C = coracoid (primary)
C′ = coracoid (secondary)
X = present
O = absent
H = homogeneous
h = heterogeneous



TEXT-FIG. 5. Pectoral girdles of iguanid lizards in lateral view. A. *Uta mearnsi.* B. *Crotophytus wislizeni.* The letters S and C indicate the suprascapula and scapulocoracoid respectively. The numbered structures are: 1. scapular foramen, 2. scapulocoracoid foramen, 3. primary coracoid foramen, 4. secondary coracoid foramen.

Two major subdivisions are recognized within this group, based upon the type of sternal arrangement. Within the line having a utiform sternum, two distinct stocks are indicated. One of these is represented by the highly specialized genus *Phrynosoma,* which lacks xiphisternal ribs, has bony spines projecting from the skull and exhibits a very peculiar hyoid apparatus. The other group contains the highly specialized genera *Callisaurus, Holbrookia* and *Uma* and the less specialized but probably more recently evolved genus *Uta.* Within *Uta,* the subgenus *Petrosaurus* appears to be most primitive although highly adapted for a rock habitat. The genera *Urosaurus, Sator* and *Sceloporus* are closely allied and differ from other sceloporines in having a urosaurine type of sternum. *Sceloporus* presumably is the most primitve genus, with the other two groups apparently derived from it.

Generic Descriptions

The genera *Urosaurus* and *Uta* have never been adequately characterized. To rectify this situation these groups are briefly described below:

Both genera share the following features in common: skull not produced posteriorly into a projection or spines; premaxillary teeth conical; anterior maxillary teeth simple, posterior maxillary teeth weakly triconodont; mandibular teeth simple anteriorly, weakly triconodont posteriorly; no teeth on palatine or pterygoid; parietal organ piercing the parietal bone posterior to frontoparietal suture; parietal very thin in region about parietal foramen; vertebrae without zygosphenes and zygantra; no scapular foramen, a scapulocoracoid foramen, a primary coracoid foramen, no secondary coracoid foramen; one or two sternal fontanels; three or four sternal ribs; xiphisternal ribs present; no parasternal ribs.

Nasal organ of the sink-trap type; no concha.

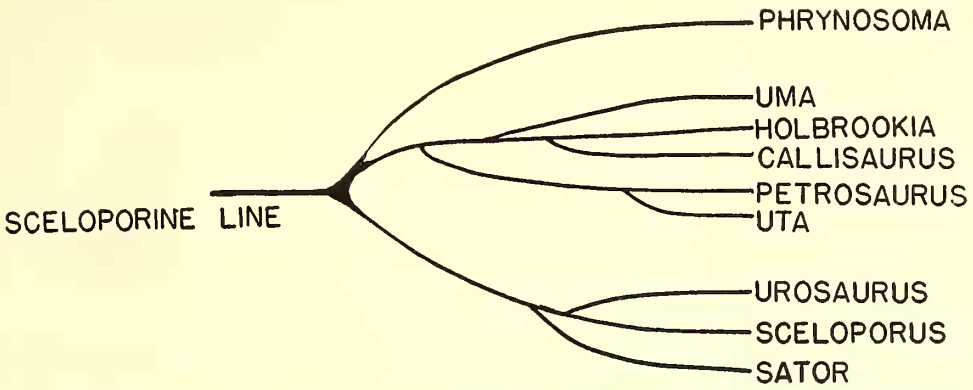
Rostral a well-developed scale; supralabials not imbricate, supercilliaries imbricate; interparietal scale large; tympanum present; auricular scales enlarged; a distinct gular fold but no gular pouch or pocket; digital lamellae not expanded to form pads, strongly keeled; toes without lateral fringes of small scales; no mid-dorsal crest of enlarged scales; some scales in paravertebral region are usually enlarged in *Urosaurus.*

Genus *Urosaurus* Hallowell, 1854

Type of genus.—Urosaurus graciosus Hallowell, 1854, by monotypy.

Distinctly different from all other iguanids in the characters mentioned above and in: (1) pectoral girdle of urosaurine type; lateral xiphisternal ribs present; (2) no supranasal scales.

Included species. — Urosaurus auriculatus (Cope, 1871); *Urosaurus bicarinatus* (Duméril, 1856); *Urosaurus clarionensis* (Townsend, 1890); *Urosaurus gadovi* (Schmidt, 1921); *Urosaurus graciosus* Hallowell, 1854; *Urosaurus irregularis* (Fischer, 1882); *Urosaurus microscutatus* (Van Denburgh, 1894); *Urosaurus nigricaudus* (Cope, 1864); *Urosaurus ornatus* (Baird & Girard, 1852); *Urosaurus unicus* (Mittleman, 1941).



TEXT-FIG. 6. Phylogenetic diagram indicating the suggested relationships between the genera of sceloporine line.

Genus *Uta* Baird & Girard, 1852

Type of genus.—*Uta stansburiana* Baird & Girard, 1852, logotype by subsequent designation of A. E. Brown, 1908, p. 117.

Distinct from groups with which it might be confused as indicated above and in having: (1) pectoral girdle of utiform type; no lateral xiphisternal ribs; (2) supranasal scales separating nasals from internasals.

Included species.—Subgenus *Petrosaurus* Boulenger, 1885: *Uta mearnsi* Stejneger, 1894; *Uta slevini* Van Denburgh, 1922; *Uta thalassina* Cope, 1863 (type of subgenus by monotypy).

Subgenus *Uta* Baird & Girard, 1852: *Uta concinna* Dickerson, 1919; *Uta martinensis* Van Denburgh, 1905; *Uta nolascensis* Van Denburgh & Slevin, 1921; *Uta palmeri* Stejneger, 1890; *Uta squamata* Dickerson, 1919; *Uta stansburiana* Baird & Girard, 1852 (type of subgenus); *Uta stellata* Van Denburgh, 1905.

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